The Veliger 30(3):257-266 (January 4, 1988)

THE VELIGER

Reproduction and Growth of the Brooding Bivalve *Transennella tantilla*

by

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Abstract. *Transennella tantilla* from the South Slough of Coos Bay, Oregon, grow and reproduce year-around. Fecundity and release of young are seasonally variable. Males are smaller than females, and the transition from male to female is progressive over a broad size range, supporting histologic studies that indicate the species is protandric. Mortality is primarily focused on the largest size classes (>2.0 mm, shell length) and appears to be caused by intense seasonal predation. Individuals of *T. tantilla* are larger and appear to be more abundant in False Bay on San Juan Island, Washington, than in the South Slough of Coos Bay. Because these differences are so striking, several life-history traits of animals from the two areas were compared. In False Bay, males reach larger sizes and females begin brooding when larger; egg size is similar, but False Bay females have smaller broods and release young at a larger size than females in South Slough. The fecundity of female *T. tantilla* from both geographic locations is a linear function of body size.

INTRODUCTION

The venerid bivalve *Transennella tantilla* (Gould, 1852) inhabits intertidal soft-substrate communities from Alaska to Lower California (KEEN, 1937). Its maximal size varies with geographic location; the reported range is 5.30–7.00 mm in shell length (GRAY, 1978; ASSON-BATRES, 1982). It has been described as a protandrous hermaphrodite (HANSEN, 1953). It is ovoviviparous, and mature females are found with broods of embryos and young in all stages of development during every season.

The associations of (1) small size and brooding and (2) small size and protandry have been observed so often that they have prompted investigators to suggest these pairs of traits may be coadapted (SELLMER, 1967; MENGE, 1975; CHRISTIANSEN & FENCHEL, 1979; CHARNOV, 1982). Because of its life-history traits (small size relative to other venerids, brooding behavior, and protandry), *Transennella tantilla* is an appropriate model for tests of coadaptation.

The purpose of this study was to provide a detailed description of the reproductive traits of *Transennella tantilla* from the South Slough of Coos Bay in Oregon. Fecundity was also monitored in females collected from False Bay on San Juan Island, Washington, where the species grows larger and appears to be more numerous. A comparison of latitudinal differences in the reproductive behavior of *T. tantilla* was of interest because differences in the size of females, brood size, or juvenile release size at the two locations could be important determinants of the increased size and apparent abundance of *T. tantilla* at False Bay.

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SAMPLING DESIGN

Data collections were designed to obtain information on protandry, fecundity, egg size, juvenile release size, seasonality of reproduction and growth, and size frequencies of *Transennella tantilla* in the South Slough of Coos Bay, Oregon. The purpose of the sampling protocol was to obtain representative data to describe these life-history parameters; it was not intended to provide data on absolute population densities within given areas.

The distribution of *Transennella tantilla* within the community is patchy (OBREBSKI, 1968). In Coos Bay, adults and juveniles occupy the upper 1–2 cm of sediment and are generally not evident until one perturbs the sediment surface. The clam secretes a byssal thread that anchors it to the grains of sediment, offering some resistence to dispersal by wave action (NARCHI, 1970). In areas of strong wave action (boat swells around the base of piers) or in

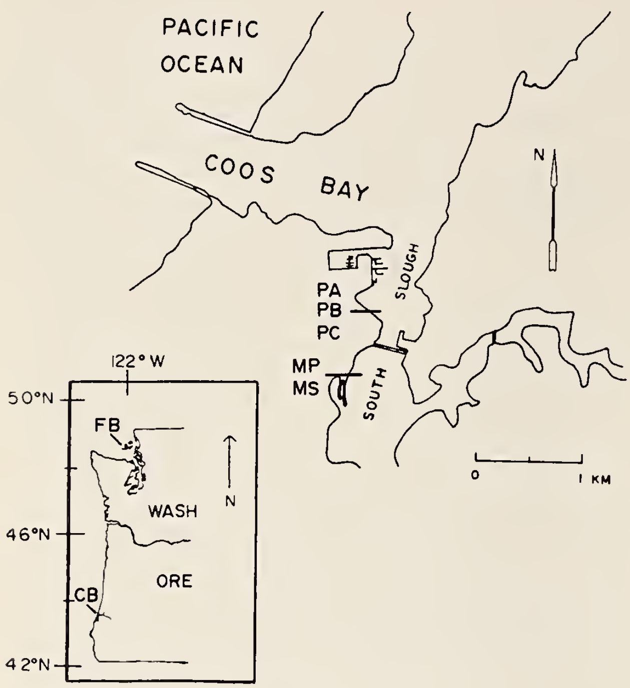

Figure 1

Map of the South Slough of Coos Bay, Oregon, indicating the location of the five study sites: PA, PB, PC, MP, and MS. Offset indicates the geographic location of Coos Bay (CB), Oregon, and False Bay (FB) on San Juan Island, Washington.

areas of fast water runoff during low tide, the clams (particularly those in the largest size classes) are swept along and deposited on the slopes of troughs sculptured by the current. In Coos Bay, the clams are subject to (1) anoxia and (2) burial by shifting sediments during seasonal storms and dredging operations.

The sampling strategy that was adopted for this study took into consideration the distribution of *Transennella tantilla* in the mudflat community and the potential for environmental factors to disrupt established populations. Time was a consideration because sieves that retain *T. tantilla* also retain a considerable amount of sediment which must be microscopically examined for removal of clams.

Size frequencies and protandry were monitored at Coos Bay by collecting a single monthly sample at each of five separated sites on the South Slough mudflat (see Study Sites section below). Given the patchy distribution of *Transennella tantilla* and the potential for a catastrophe (such as storm waves, sediment deposition, or human activity) to wipe out the population at a particular site, it was preferable to regard the mudflat as a single large site and to collect samples at five discrete locations. To allow tests of within sample disparity at each mudflat location, each sample was divided into three equal subsamples in the field, and each subsample was collected and analyzed separately.

A caging experiment was designed to provide qualitative, rather than quantitative, information on the time of growth and release of juvenile *Transennella tantilla* at Coos Bay.

For geographic comparison of female fecundity, samples of *Transennella tantilla* were periodically hand collected from Coos Bay and False Bay. Details and schedules specific to this sampling procedure and those discussed above are described in the Materials and Methods section below.

STUDY SITES

Field studies were conducted at five defined sites (PA, PB, PC, MP, and MS) on the South Slough mudflat of Coos Bay, Oregon (43.8°N). The South Slough empties into the main channel of Coos Bay, approximately 1.3 km from the mouth of the bay (Figure 1). The sites were picked because they were representative of areas where *Transennella tantilla* is commonly found on the South Slough mudflat. All sites were accessible on most low tides and were relatively free of human disturbance. The tidal heights were similar at each location: +0.58 m, +0.34 m, +0.73 m, +0.76 m, and +1.13 m above mean lower low water at sites PA, PB, PC, MP, and MS respectively.

Transennella tantilla was also collected bimonthly at False Bay on San Juan Island, Washington (48.5°N, Figure 1).

MATERIALS AND METHODS

Monthly samples were collected from each of the five sites on the South Slough mudflat from February to December 1981. *Transennella confusa* also occurs in the South Slough of Coos Bay (Gray, 1982), but only *T. tantilla* was used in this study. Each month, the sites were searched to determine if major changes in clam densities had occurred. Areas where obvious changes were noted (*i.e.,* areas that were anoxic, traversed by streams, or where clams were absent) were excluded, and a sample was selected by randomly tossing a circular sampler (diameter = 35.7 cm, area = 0.1 m^2) onto the substrate in another area within the site. Sediment to a depth of 4 cm was removed from each subsample and sieved with a 500-μm mesh screen. This mesh size was chosen because it retained animals greater than or equal to 800 μm in shell length and an amount of sediment that could be microscopically sorted in a reasonable amount of time. Sieved subsamples were preserved in 70% isopropyl alcohol.

Shell lengths of all clams in the preserved subsamples were measured with an ocular micrometer and the results were grouped into 16 size classes by site and by month. A total of 2099 *Transennella tantilla* were removed from the subsamples collected at sites PA, PB, MP, and MS during the months of March, April, May, July, August, October, and December, and were dissected to determine the size range of males and females. When brooded embryos were not present, sex was determined by examining gonads. Testes in preserved specimens were white, translucent, branching structures; ovaries were globular and contained white or light yellow eggs that were irregular in shape.

Because of the difficulty of dissecting smaller specimens, only individuals greater than or equal to 1.85 mm in shell length were sexed. It was possible to identify the sex of over 98% of the clams examined. The other 2% were either sexually undeveloped or were infected with gonad parasites that obscured identification. Questionable specimens were not included in the sex ratio analysis. Clams from samples collected at site PC were not sexed because fewer than 25 animals were 1.85 mm or longer in the entire 0.1-m^2 sample (data for all subsamples combined) for five of the seven months considered.

To assess directly the time of growth and release of offspring in Coos Bay, *Transennella tantilla* individuals were retained in the field in cages made of plastic tubes, 3.0 cm in diameter × 4.0 cm in height, with fabric affixed to each end (approximate mesh size = 0.35 mm, the height of newly released juveniles). A detailed description of cage construction is available in Asson-Batres (1982). Each cage was half-filled with supratidal bay sand, and one measured clam, 1.0–4.4 mm in shell length, was added. The cages were brought to the laboratory for examination on a monthly or bimonthly schedule. They were held for less than 24 h in outdoor, running seawater aquaria before and after examination. The lengths of all survivors were recorded. Because time was a factor and females cannot be identified externally, only the sediment in cages with survivors greater than 2.67 mm in shell length was microscopically examined for the presence of offspring. Survivors (with the exception of offspring) were returned to their cages with fresh sand and dead clams were replaced. Eight trays of 28 cages each were followed on the South Slough mudflat from December 1980 to June 1981; five trays of 28 cages each were followed from June to December 1981.

To determine female size at maturity, brood size, and the relationship between fecundity and female size or season, specimens of *Transennella tantilla* were collected by hand from the South Slough mudflat in July 1980 and monthly from October 1980 to December 1981. The organisms were retained at 4°C in glass culture dishes filled with fresh seawater. Female lengths were measured, and embryos were removed from the gills and counted. Egg diameters and embryo lengths were measured to the nearest 0.01 mm under 200× magnification. Whole animal (shell included) weights of *T. tantilla* collected during October, November, and December 1980 were determined. Wet weights were recorded to the nearest 0.1 mg.

Samples of *Transennella tantilla* were hand collected from False Bay in May 1980, and bimonthly from November 1980 to October 1981. Living clams were retained and analyzed as described above.

RESULTS

Subsample Analysis

A single classification analysis of variance with repeated measures (Phillips, 1978) was carried out to compare subsample densities. Data from each site were analyzed independently. For a given month, at a given site, subsample densities were always comparable ($P > 0.60$). As a result, subsample data were combined for further analyses.

Table 1

Sex structure of the *Transennella tantilla* population at sites PA, PB, MP, and MS on the South Slough of Coos Bay, Oregon, sampled from March to December 1981.

Size class (mm)*	n†	% male
1.85–2.07	758	89
2.15–2.37	592	70
2.44–2.66	326	36
2.74–2.96	187	12
>2.96	236	1

* Shell lengths were measured in divisions with an ocular micrometer. Conversion of divisions into mm (×100, one division = 0.074 mm) results in discontinuous size-class groupings.

† n indicates the number of animals examined.

Size Range of Males and Females

The wet tissue weight (WTW, mg) of *Transennella tantilla* was related to shell length (SL, mm) by the regression, $\log_{10}WTW = 3.04 \log_{10}SL - 0.54$ ($SD_{regr} = 0.06$; $r^2 = 0.98$; $n = 42$). Because there was a good correlation, the anteroposterior dimension (length) was used as an indicator of clam weight.

Shell lengths of *Transennella tantilla* ranged from 0.55 to 5.33 mm. The largest male found during the study was 3.48 mm (dissected live, January 1981); the smallest female found was 1.70 mm long (dissected live, July 1981: the specimen had ripe ovaries, but no brood). The transition from male to female occurred over a broad size range, with the majority of males less than 2.37 mm long (Table 1).

Seasonal Effects on Fecundity

An average (±SD) of 36 (±13) broods were counted monthly (range = 15–56). Broods ranged in size from one egg in each of three clams, 2.07, 2.29, and 2.37 mm in length, to 327 embryos in a specimen 5.10 mm in length. The smallest brooding female was 1.92 mm, and the largest was 5.33 mm.

Females of all sizes were found with broods throughout the year (Figure 2, Table 6). Broods contained uncleaved eggs and embryos with and without shells. Uncleaved eggs and the smallest embryos were held tightly together in packets in the gills; older embryos were more loosely connected to the rest of the brood. Eggs ranged from 0.21 to 0.26 mm in diameter. The largest embryos observed were 0.55 mm in shell length.

Fecundity was a linear function of adult size (Figure 2). The coefficients of determination (r^2) for least-squares regression were greater than 0.76 for all months except March, August, and November 1981, when they were

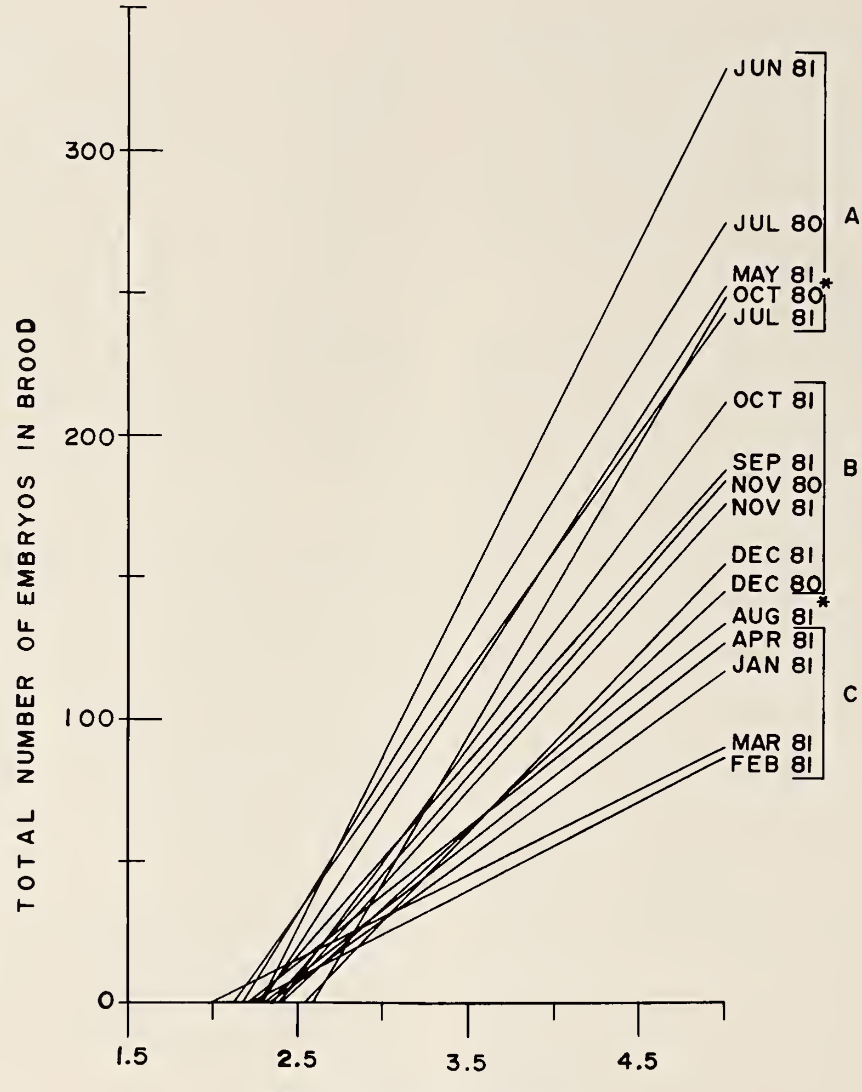

Figure 2

Seasonal change in the fecundity-size relationship of *Transennella tantilla* from the South Slough of Coos Bay, Oregon. Each line is the best fit regression line for data analyzed by least squares. Slopes range from 30 to 113; coefficients of determination (r^2) range from 0.61 (August 1981) to 0.94 (December 1980) ($P < 0.001$ for all regressions). The regression data were categorized into three seasonal groups (A, summer; B, fall; and C, winter–spring) and compared by ANCOVA ($P < 0.001$). *Data for August 1981 were assigned to the summer group and those for October 1980 to the fall group.

0.67, 0.61, and 0.69 respectively. All regressions were highly significant ($P < 0.001$).

Fecundity was seasonally variable (Figure 2). Data collected during the three seasons delineated in Figure 2 were combined and compared by an analysis of covariance (ANCOVA). Brood sizes of females of a given length were significantly larger during summer months than during late winter–early spring months and were intermediate in size during fall months (ANCOVA, $P < 0.001$).

The seasonal change in brood size occurred in females of all sizes and was similar during both years. Independent comparisons of data collected during the same months (July, October, November, and December of 1980 and 1981) were made using ANCOVA. There were no significant differences between any of the monthly pairs ($P > 0.10$). An inconsistent depression in brood size during August 1981 could not be explained.

In all but two monthly samples from Coos Bay, 2–24%

of the specimens examined had trematode sporozoites containing cercariae attached to their gonadal tissue. Parasitized females were randomly matched with non-parasitized females by shell length and collection date to correct for animal size and seasonal effects on brood size. Regressions of brood size on adult length for the resulting subset of 75 pairs of females were compared by ANCOVA. The brood sizes of animals with infected gonads were notably depressed (uninfected clams: Brood Size = 68 × Adult Length (mm) − 156, r^2 = 0.53; infected clams: Brood Size = 4 × Adult Length (mm) − 8; r^2 = 0.03; $P < 0.001$). As a result, females with infected gonads were excluded from the fecundity analyses above.

Release of Juveniles

Individual females (>2.67 mm long) maintained in field enclosures at Coos Bay released young during 11 of the 12 months they were monitored (Figure 3). Only two females survived during October and neither released young. The average (±SD) number of offspring released per female per month was 3 (±3) (Asson-Batres, 1982) which is lower than might be expected given the number of embryos known to be present in broods.

Periodic sediment burial and algal overgrowth led to anoxia in some cages. The sediment within these cages was black, indicating the presence of sulfide. Dead clams had blackened shells that were still articulated. Broods of dead eggs and shelled embryos were still present in dead females from these cages.

After one to two months of field exposure, cages that were sulfide-free mimicked the surrounding field community, with amphipods, cumaceans, tanaids, polychaetes, nemerteans, and nematodes established in the cage sediment. After field exposure, clams in these cages were alive except during October, when survivorship was inexplicably low.

It is unlikely that unnatural cage conditions induced females to release offspring because (1) shelled embryos of release size were found in the body cavities of dead females and (2) some living clams greater than 2.67 mm long (presumably the majority of these clams were female, see Table 1) did not release offspring (Figure 3). Thus, while cage artifacts may have depressed release rates, the results provide direct evidence that *Transennella tantilla* can release young year-around.

Representative monthly size-frequency distributions of *Transennella tantilla* collected from two of the South Slough study sites are presented in Table 2A, B (data from the other three sites are available in Asson-Batres, 1982). The first size class, which includes clams 0.59–0.74 mm in length, is underrepresented because the 500-μm mesh sieve did not retain newly released *T. tantilla* (the minimum shell dimension, clam height, is less than 0.5 mm). Thus, a lag of about one month exists between the actual time of juvenile release and the time when clams of the smallest size classes show up in the samples. As an example, the

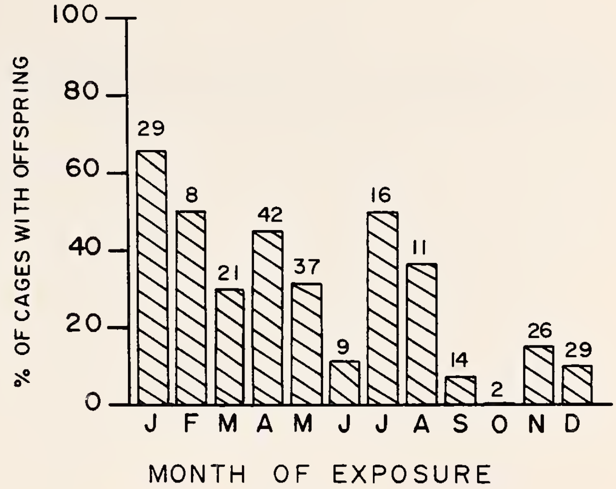

Figure 3

Percent of caged females (>2.67 mm long) with offspring. Field enclosures were maintained in the South Slough of Coos Bay, Oregon, and monitored monthly during 1981. Only cages with surviving females were examined for presence of offspring. The total number of cages examined each month is indicated above each bar.

majority of clams making up the second size class in the samples collected at site PA during March and April were probably released during February or March.

Juvenile clams were found at one or more sites during every month. Because the absolute number of juveniles is underrepresented in the sample (owing to the method of collection, see above), the second size class (0.81–1.04 mm) offers a better indication of the peak periods of juvenile release (Table 2A, B; Asson-Batres, 1982). Taking the lag period into consideration, peak release of juveniles occurred at sites PA, MP, and MS during February through April, and again at sites MP and MS during July and August. Except for a single surge in release of young at site PC during April, juvenile release was consistently low at sites PB and PC throughout the study period.

Growth

Individual *Transennella tantilla,* retained in cages on the Coos Bay mudflat, grew every month of the year (Table 3). The absolute change in shell length ranged from 0.07 to 0.56 mm per clam per month.

Distinct rings and zones were not present on the shells of animals in monthly field collections, suggesting that shell growth was continuous.

Mortality

A decline in the densities of large *Transennella tantilla* occurred at sites MP, PA, and PB from June to September. This is evident in Table 4, which compares the number (or relative percent) of clams greater than 2.0 mm in shell

Table 2

Size-frequency data for *Transennella tantilla* collected from two sites in the South Slough of Coos Bay, Oregon, during 1981. The number of clams comprising each size class are presented as percentages of the total number of clams present in the 0.1-m^2 sample. Sample sizes are included at the bottom of the table so that raw numbers can be generated, if desired.

Part A. Site PA

Size class (mm)	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
0.59–0.74	2	1	1	0.7		0.5	0.4	0.7		0.6
0.81–1.04	51	48	23	24	21	12	5	4		20
1.11–1.33	29	25	44	33	23	23	11	4	7	8
1.41–1.63	8	11	22	31	37	26	19	7	1	2
1.70–1.92	4	6	7	10	17	27	26	19	3	6
2.00–2.22	2	3	2	0.7	3	11	23	30	8	13
2.29–2.52	2	3	1	0.5		1	14	20	24	19
2.59–2.81	0.8	1	0.4				1	11	23	13
2.89–3.11	0.2	1	0.3	0.2				4	11	14
3.18–3.40	0.5	0.3	0.4					0.7	13	4
3.48–3.70	0.3								3	0.6
3.77–4.00	0.3	0.1	0.1	0.2					7	
4.07–4.29	0.2	0.1							1	
Total number of clams in sample	593	1172*	1018	410	342	376	203	152	75	158

Part B. Site MP

Size class (mm)	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
0.59–0.74	0.2		4	2	0.7	6	6	1	0.5	0.3	0.2
0.81–1.04	27	11	43	35	19	32	62	43	13	8	14
1.11–1.33	18	10	16	30	26	27	15	35	22	5	19
1.41–1.63	19	14	9	10	27	20	7	13	26	14	22
1.70–1.92	11	17	9	6	13	10	5	5	21	27	20
2.00–2.22	12	24	8	6	5	3	3	2	9	24	13
2.29–2.52	6	14	6	5	3	1	1	1	4	14	5
2.59–2.81	4	5	3	2	2	1	0.5	0.6	2	5	3
2.89–3.11	1	2	1	2	2	0.6	0.2		1	3	0.8
3.18–3.40	0.2	0.7	0.7	1	1	0.3			0.3	0.8	0.7
3. 48–3.70	0.8	0.7	0.1	0.4	0.7					0.5	0.3
3.77–4.00	0 .2	0.7					0.1				0.1
4.07–4.29				0.2	0.1						
4.37–4.59				0.1	0.1						
Total number of clams in sample	479	606	1418*	1355	1524	1163	929	1042	663	600*	1147

* Estimate based on two subsamples of 0.03 m^2 each.

length in monthly samples from the sites. Pre-decline densities of large clams were re-established at the sites during fall and winter months. Clams less than 2.0 mm in shell length did not decline during the summer at sites MP, PA, and PB (data not shown).

There was a precipitous decline in all sizes of *Transennella tantilla* at site PC in May (ASSON-BATRES, 1982). During June and July, repeated samples were checked for the presence of *T. tantilla*, but specimens retained by the 500-μm mesh screen were not present. Concomitant with the disappearance of live *T. tantilla* from the site was the appearance of numerous *T. tantilla* half-shells and shell fragments. Clams greater than 2.0 mm in shell length did not reach pre-decline densities at site PC (Table 4). A year later (June 1982), numerous (>10) samples were sieved (500-μm mesh) at the site and only one living *T. tantilla* was found. Such intensive sieving before the crash would have retrieved hundreds of clams visible to the naked eye.

Neither large (Table 4) nor small *Transennella tantilla* declined in number at site MS during summer months.

Life-History Characteristics of *Transennella tantilla* from False Bay

Fecundity was a linear function of adult size and was seasonally variable (Table 5). Females of a given size in False Bay had smaller broods than females of comparable size in Coos Bay and, although females in False Bay reached

Table 3

Growth of *Transennella tantilla* retained in field enclosures in the South Slough of Coos Bay, Oregon, during 1980–1981. One clam present per cage.

Month(s) of exposure	Number of survivors	% of survivors that grew	Change in length (mm) mean ± SD*
Dec–Feb	29	66	0.12 ± 0.06
Jan	54	72	0.11 ± 0.06
Jan–Mar	23	65	0.13 ± 0.06
Feb	26	15	0.06 ± 0.02
Feb–Apr	25	88	0.16 ± 0.10
Mar	48	75	0.11 ± 0.06
Mar–May	28	57	0.25 ± 0.20
Apr	66	53	0.15 ± 0.08
Apr–Jun	4	75	0.30 ± 0.20
May	69	38	0.12 ± 0.08
May–Jul	11	55	0.23 ± 0.10
Jun	21	48	0.11 ± 0.04
Jul	34	59	0.18 ± 0.14
Aug	26	81	0.12 ± 0.06
Sep	33	73	0.10 ± 0.04
Oct	4	75	0.12 ± 0.04
Nov	46	80	0.17 ± 0.08
Dec	42	7	0.07 ± 0.00

* The mean includes only those clams that showed an increase in length.

larger sizes than females in Coos Bay, the maximum brood sizes of False Bay animals were smaller than those of Coos Bay females during four of the six months sampled (Table 6).

Of the clams from the bimonthly collections from False Bay 2–17% were infected with trematode parasites. Parasitized females had significantly reduced brood sizes (ANCOVA, $P < 0.001$) and were excluded from the fecundity analyses.

Table 4

Number (%) of *Transennella tantilla* greater than 2.0 mm in shell length in monthly samples collected from each of the five study sites in the South Slough of Coos Bay, Oregon, in 1981.

Month	PC	PA	PB	MP	MS
Feb	198 (34)	—	44 (51)	116 (24)	38 (28)
Mar	229 (49)	37 (6)	71 (49)	285 (47)	68 (15)
Apr	266 (48)	100 (9)	422 (69)*	267 (19)	47 (7)
May	3 (2)	43 (4)	41 (59)	226 (17)	44 (7)
Jun	0 (0)	7 (2)	8 (24)	212 (14)	82 (18)
Jul	0 (0)	10 (3)	7 (7)	69 (6)	167 (27)
Aug	4 (7)	45 (12)	4 (3)	45 (5)	57 (27)
Sep	27 (73)	77 (38)	40 (49)	37 (4)	62 (11)
Oct	18 (83)	100 (66)	62 (67)	108 (16)	93 (24)
Nov	50 (94)	62 (82)	46 (49)	284 (47)	—
Dec	25 (80)	100 (64)	47 (30)	263 (23)	133 (38)

* The April sample size was spuriously high because the sample was collected from the slope by a pier where wave action deposited large individuals of *T. tantilla*.

Table 5

Brood size of *Transennella tantilla* collected from False Bay on San Juan Island, Washington. Regression data are for brood size (B) plotted over adult length (L) ($P < 0.001$ for all regressions).

Date	n*	Equation	r^2
Nov '80	31	B = 77L − 263	0.77
Feb '81	36	B = 20L − 62	0.85
Apr '81	65	B = 30L − 90	0.72
May '80	27	B = 41L − 128	0.64
Jun '81	48	B = 67L − 202	0.89
Aug '81	48	B = 82L − 303	0.85
Oct '81	39	B = 37L − 127	0.55

* n indicates the number of animals examined.

DISCUSSION

The field enclosure studies provide direct evidence that *Transennella tantilla* can reproduce and grow year-around in the South Slough of Coos Bay, Oregon. The results from monthly field samples support these observations. The presence of juvenile clams in all field collections supports the contention that release is continuous. Because it is known that variations in growth rate are recorded by distinct zones or rings on bivalve shells (Nayar, 1955; Jones, 1983), the absence of such rings on the shells of *T. tantilla* in this location suggests that growth is continuous.

Continuous release of young by *Transennella tantilla* is not exceptional; other bivalves in northern waters also spawn year-around. *Mytilus californianus* spawns all year off the west coast of the United States (Whedon, 1936; Suchanek, 1981) and at least part of the populations of *Astarte borealis* and *A. elliptica* in the Baltic Sea carry eggs and sperm year-around and spawn for a period of up to eight months (von Oertzen, 1972).

A majority of the clams between 1.85 and 2.37 mm in shell length from the sites in South Slough were males, whereas larger animals were predominantly females (Table 1). These results, along with Hansen's (1953) demonstration (using histological techniques) that some individuals were in the process of a sex reversal, provide strong support for protandry in this species. The sex structure of the population was similar throughout the year at all sites, which suggests that sex reversal occurs throughout the year. The male-to-female sex ratios of populations sampled at sites PA and PB were 55:45 and from sites MP and MS were 61:39 (Asson-Batres, 1982). The proportion of males at each site is probably an underestimate because many animals smaller than the cut-off length of 1.85 mm likely were males.

Protandry is predicted when reproductive success is independent of size for males, but proportionally greater for large females than for small ones (Ghiselin, 1969; Warner, 1975). Model simulations that assume these conditions predict that the smallest mature individuals in a

Table 6

Comparison of the mean ($\bar{x}$) brood size of *Transennella tantilla* by shell length (mm), month, and geographic location. The number (n) of animals examined is indicated. The animals were collected from False Bay on San Juan Island, Washington, and the South Slough of Coos Bay, Oregon.

Month	Female size class (mm)	False Bay $\bar{x}$	False Bay (n)	Coos Bay $\bar{x}$	Coos Bay (n)
Nov '80	2–3	—	—	24	(5)
	3–4	31	(8)	74	(9)
	4–5	74	(11)	127	(4)
	5–6	150	(12)	—	—
Feb '81	2–3	—	—	11	(16)
	3–4	9	(17)	32	(24)
	4–5	27	(19)	56	(4)
	5–6	—	—	88	(3)
Apr '81	2–3	3	(2)	20	(15)
	3–4	10	(25)	51	(32)
	4–5	37	(30)	96	(8)
	5–6	85	(8)	—	—
Jun '81	2–3	1	(6)	35	(26)
	3–4	12	(10)	150	(19)
	4–5	92	(12)	265	(5)
	5–6	169	(15)	275	(1)
	6–7	185	(5)	—	—
Aug '81	2–3	—	—	15	(20)
	3–4	6	(18)	53	(16)
	4–5	26	(17)	129	(1)
	5–6	145	(11)	—	—
	6–7	232	(2)	—	—
Oct '81	2–3	—	—	20	(6)
	3–4	21	(2)	73	(21)
	4–5	39	(29)	143	(1)
	5–6	61	(8)	—	—

population will be male. At some larger size, it will be more profitable to be female and, at this point, a change in sex will occur. Field studies of protandrous shrimp and plants offer evidence that the model is realistic (CHARNOV, 1979; POLICANSKY, 1981). Because large females of *Transennella tantilla* produce proportionally more embryos than small females, it is tempting to speculate that the model offers an appropriate explanation for protandry in this species. It is of interest that *Gemma gemma,* also a small (5 mm, maximum shell length) brooding venerid is dioecious. Female *G. gemma* begin brooding at about 2.0 mm in length, and fecundity increases logarithmically with female size. Juveniles are released when they are fully developed. Their life-span is thought to be 2 yr (SELLMER, 1967; GREEN & HOBSON, 1970). Although a positive correlation between fecundity and female size exists in both species, *T. tantilla* is a sex-changer and *G. gemma* is not. It is currently not possible to test the relative interspecific productivity of males. It may be that reproductive success is size-dependent for male *G. gemma* and size-independent for male *T. tantilla.*

The summer decline in densities of *Transennella tantilla* from four of the five study sites in Coos Bay was most likely due to predation. Juvenile *Cancer magister* (Dana) (13–30 mm in carapace width) forage for *T. tantilla* in the South Slough of Coos Bay, Oregon (ASSON-BATRES, 1986). When feeding on the clams, this crab characteristically separates the valves, leaving one half-shell intact (ASSON-BATRES, 1986). The megalops of *C. magister* were present in the Coos Bay estuary from mid-March to the end of May of 1981 (ROWELL, 1981) and would have metamorphosed to first instar juveniles throughout April to June. The coincidental disappearance of the clams and appearance of juvenile *C. magister,* and the concomitant appearance of half-shells and shell fragments at the site where the clams were found when alive, suggest that juvenile *C. magister* was a factor in the summer decline of *T. tantilla.* In support of this interpretation, it has been reported that small bivalves are a major part of the diet of first year *C. magister* (STEVENS *et al.,* 1982).

Shore birds and bottom-feeding fish that appear seasonally may have also contributed to the decline of *Transennella tantilla.* OBREBSKI (1968) indicated that the gut contents of unidentified shore birds collected near Bodega Bay contained *Transennella.* VIRNSTEIN (1977) reported that spot fish, *Leiostomus xanthurus,* were important predators on juvenile clams (1–3 mm, shell length) in the York River of Chesapeake Bay. Whether birds or fish feed seasonally on *T. tantilla* in South Slough has not been investigated. Juveniles of other species of crabs may have also preyed on *T. tantilla* during the summer, but none are likely to have been as abundant as juvenile *C. magister.*

The population decline of the large size classes at three of the five sites, and the population crash of all sizes at one site, suggest that mortality may be unpredictable for this species. Direct release of relatively immobile young can lead to the formation of groups of animals separated in space (patches). This could provide a refuge from predators, as they may overlook a prey patch. The stable population density observed at site MS during this study, concurrent with the decline of population densities at other sites, is consistent with such a prediction.

Individuals of *Transennella tantilla* from False Bay reach lengths up to 1.3 mm longer than their conspecifics in Coos Bay (Table 7). According to GRAY (1978), *T. tantilla* in Tomales Bay, California (38.4°N) reach 7.00 mm in length. Thus, the size of *T. tantilla* at False Bay, Coos Bay, and Tomales Bay is not correlated with the change in latitude.

Transennella tantilla is conspicuously distributed over much of the tideflat in False Bay. At mean lower low water, where the species is most dense in False Bay, it is a numerically dominant species (PAMATMAT, 1969; BRENCHLEY, 1981). In contrast, *T. tantilla* is smaller, less exposed, and distributed in isolated patches on the mudflat in the South Slough of Coos Bay, giving the impression

Table 7

Comparisons of life-history traits of *Transennella tantilla* from False Bay on San Juan Island, Washington, and the South Slough of Coos Bay, Oregon. Observations are personal except as indicated in parentheses. AB = ASSON-BATRES, 1982; H = HANSEN, 1953.

	False Bay, Washington	Coos Bay, Oregon
Latitude	48.5°N	43.8°N
Shell length	0.65–6.60 mm	0.55–5.30 mm
Male size range	1.50–4.60 mm (H)	<1.85–3.48 mm
Female size range	>2.80 mm	>1.70 mm
Female reproductive behavior	Brood present all year; fecundity a linear function of size	Brood present all year; fecundity a linear function of size
Maximum brood size (adult length)	293 (5.6 mm)	327 (5.1 mm)
Diameter of uncleaved egg in brood chamber	0.25 mm (H, AB)	0.21–0.26 mm
Juvenile release size	0.65 mm (H, AB)	0.53–0.55 mm

that it is less abundant there than in False Bay. If abundance is greater in False Bay than in Coos Bay, it is not a result of increased brood sizes: females of similar size brood fewer embryos in False Bay than in Coos Bay (Tables 6, 7).

Females in both locations produce eggs of similar size (Table 7), but in False Bay, young are released at a larger size. The energetic costs of producing offspring should be equal at the two locations, if, as it is assumed (HANSEN, 1953), embryos receive no nutrition from the parent during development. In this species, then, egg size appears genetically fixed, whereas other life-history traits are more plastic.

Parasitized animals from Coos Bay and False Bay had significantly smaller brood sizes. KABAT (1984) reported that 31% of the brooding females he examined from False Bay hosted parasites and produced only 40% as many embryos as non-parasitized females of the same size. In this study, the percentage of clams infected with gonad trematodes was extremely variable: 0–24% of the specimens collected at Coos Bay, and 2–17% of those from False Bay had parasitized gonads. There was no apparent correlation between the number of parasitized animals and the collection date (personal observation, unpublished).

Factors that restrict the productivity of female *Transennella tantilla* in Coos Bay and False Bay are the animal's life-span, the incidence of parasitism, and seasonal effects on egg production, embryonic growth, and juvenile release. Senility does not limit productivity because all non-parasitized, mature females are found with broods, and the oldest (largest) females have the largest broods. It is uncertain whether the allometry of egg production and brooding (STRATHMANN & STRATHMANN, 1982) limits productivity in *T. tantilla*. The linearity of the correlations between brood size and female size (recall that wet weight is correlated with length, see Results above) and the capacity of the organism to adjust its brood size upward during some seasons suggest that large *T. tantilla* have ample space to brood as many gametes as they are capable of producing. However, differences in the brood structures of animals from Coos Bay and False Bay may argue against this interpretation; a limitation in brood space could constrain females to brood either higher numbers of small young (as in Coos Bay) or lower numbers of large young (as in False Bay).

In summary, *Transennella tantilla* is a small, protandric, brooding bivalve that grows and reproduces year-around in the South Slough of Coos Bay, Oregon. It appears to be subject to intense seasonal predation by incoming settlements of juvenile *Cancer magister* and possibly shore birds and bottom-feeding fish. Maximum adult size is geographically variable, but there does not appear to be a correlation between animal size and latitude. Brood size, juvenile release size, age at maturity, and the size range of males and females vary between geographic sites (Table 7). Whether the comparative flexibility observed in many of the life-history characteristics of this species (Table 7) represents genetic differences or physiological adaptability to locally induced pressures has not been investigated. In this regard, a reciprocal transplant experiment and electrophoretic comparative analysis of the populations would be of interest.

ACKNOWLEDGMENTS

I thank P. W. Frank for encouragement and advice throughout the study and for assistance with preparation of the manuscript; R. R. Strathmann and R. I. Ingermann for helpful discussions; P. Rudy, Director of the University of Oregon Institute of Marine Biology, E. Kozloff, Acting Director of Friday Harbor Laboratories, and their staff for providing research facilities; and S. Batres for assistance in the design and construction of the experimental field cages. The field research was partially funded by a grant-in-aid from Sigma Xi. Preparation of the manuscript was supported in part by PHS Research Grant HD 15308.

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